ARE PITFALLS BIASED? A COMPARISON OF CARABID COMPOSITION FROM PITFALL TRAPPING AND HAND SEARCHING IN FOREST HABITATS

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ABSTRACT

There have been concerns over potential biases from the use of pitfall trapping in carabid research. However, few studies have compared the results obtained from pitfall traps with those of other methods. Forty-five paired pitfall traps and hand searching samples were obtained from nine habitats in Thetford Forest, Breckland, for comparison. With much less effort, pitfall traps produced over three times the number of individuals as hand searching, although both methods produced the same number of species. *Harpalus rufipalpis* Sturm, *Amara lunicollis* Schiödte and *Notiophilus aquaticus* L. were over-represented in pitfall traps. Overall, pitfall trapping preferentially captured larger species (⩾8 mm) while hand searching resulted in more individuals of smaller species (<8 mm). Despite these biases, both methods gave a qualitatively similar ordination of community composition across habitats.

Keywords: pitfall traps, hand searching, biases, activity-abundance, carabid assemblage

INTRODUCTION

Pitfall trapping has been one of the most extensively used methods for carabid research (Desender & Maelfait, 1986). It is low-cost, simple to carry out and relatively efficient at catching, so that it is possible to obtain a greater number of individuals with relatively less effort than other methods (Southwood & Henderson, 2000). As this group tends to show slow species rarefaction (i.e. even when many individuals have already been examined, catching a few more can still produce additional species), it is important to obtain sufficient material when studying species composition. Consequently, pitfall trapping has been widely adopted in studies of carabid abundance and assemblage composition (Thiele, 1977).

Despite the widespread acceptance of pitfall trapping in carabid research, there are a number of concerns regarding potential biases that can arise with this method. The catch efficiency of pitfall traps is influenced by other factors in addition to population size (Adis, 1979; Southwood & Henderson, 2000). The catch size of pitfall trapping is a function of both the density of the population and the activity of individuals (Briggs, 1960; Mitchell, 1963; Thiele, 1977). Greenslade (1964) showed that the size, behaviour and activity strata of different carabid species can all influence their trapability. Different species have different susceptibilities toward traps, and some ‘investigative’ behaviours (i.e. suspending over the edge of the trap with hind tarsi or walking down inside the trap and climbing out again) can affect capture rates (Hawthorne, 1994). Even within the same species, individual beetles which moved rapidly were more likely to be captured in laboratory experiments (Morrill *et al.*, 1990). Moreover, considering the behavioural change of species in response to microhabitat, the comparison of carabid faunas between habitats that are structurally different based on pitfall trapping alone raises further concerns (Topping & Sunderland, 1992; Hawthorne, 1994; Andersen, 1995).

Details of the traps such as size, material and type of preservative or attractant, also influence capture efficiency (Luff, 1975; Benest, 1989; Holopainen, 1990; Morrill *et al.*, 1990; Spence & Niemelä, 1994; Work *et al.*, 2002). This can make it hard to compare results from different experiments and highlights the importance of standardising protocols within any one study.

Andersen (1995) stated that "Although pitfall traps have been used extensively in ecological field studies of carabid beetles, few studies have made direct comparisons between this method and absolute quantitative methods such as quadrat sampling". By a comparison of pitfall trapping and soil sampling, Briggs (1960) discovered a strong relationship between temperature and catching rates of *Harpalus rufipes* De Geer and *Feronia melanaria* Illiger and suggested that the increase of locomotor activity of beetles with increasing temperature was the main determining factor of the pitfall trapping result. Spence & Niemelä (1994) compared samples taken from pitfall trapping and a litter-washing technique and found pitfall samples yielded mostly large-sized beetles. By comparing the results from mark–release–recapture to those from pitfall trapping, Hawthorne (1994) concluded pitfall trapping was useful for the comparison of individual species abundance between habitats as long as the species behaviour did not differ significantly in response to habitat differences.

In this study, the relative abundance of species collected by pitfall trapping was compared with the absolute density estimated by hand searching. Samples were taken from different habitat structures in Thetford Forest, Breckland, to see if microhabitat influenced both methods similarly. Results are discussed in relation to possible biases and the usage of both methods.

Methods

Pitfall trapping and hand searching were carried out in June, 2002 in nine locations within Thetford Forest, a lowland managed coniferous forest located in Breckland, eastern England (TL 7882). Sampling was carried out in six recently re-planted clearfelled stands (planting year ranging from 1997 to 2002), one felled but unplanted stand (felled trees removed but ploughing of planting rows had not yet been carried out, referred to as planting year 2003), one ride margin supporting heathland-like vegetation (ride margin), and one stand with 54 year-old trees (mature forest stand).

At each of the nine sampling locations, five pitfall traps were placed about 30 metres apart along a single line transect. Pitfall traps were 7.5 cm in depth, 6.5 cm in diameter transparent plastic cups containing 50 ml of ethylene glycol. Each trap was kept separately when collecting, however for analysis, results of each transect were pooled to represent each habitat. Pitfall traps were set up between 21 and 25 June, 2002 and collected five days later. The mean ($\pm$SD) maximum temperature measured from eight of the stands (no measurement was taken from the planting year 2000 stand) during this sampling period was 30.5 ± 1.8 °C and the minimum temperature was 0.75 ± 3.3 °C. The large diurnal range and low minimum temperature are not atypical for Breckland, which is famous as a semi-continental region of Britain where frosts may occur in any month of the year.

Hand searching was conducted about two metres from each pitfall trap. Searching was carried out within a 100 cm long, 80 cm wide and 30 cm high hardwood frame, placed to prevent beetles from escaping during the hand searching period. All ground vegetation, debris and the upper few centimetres of sand were removed and searched destructively in order to obtain all the carabids within each quadrat. Quadrat samples from each transect were pooled for comparison with those from pitfall traps. To reduce the bias caused by temporal dynamics, hand searching was carried out the day after pitfall traps were collected. Seven of the nine transects were hand-searched during daytime on 29 June, 2002, ride margin and mature forest stands were done the following day. Carabids were identified to species mainly according to Lindroth (1974) with nomenclature updated following Luff & Duff (2002).

Chi-square tests were used to compare the size spectra of captured carabids between the two methods. The species composition of different habitats was analysed by ordination, using correspondence analysis conducted in CANOCO for Windows 4.5 (ter Braak & Smilauer, 1997). Due to low numbers of individuals captured in each stand, samples taken from clear-fells of similar planting years were pooled prior to correspondence analysis. Correspondence analysis was therefore conducted on five pooled pitfall samples and their corresponding five hand searched samples. The relative position within the ordinations, of samples obtained from different habitats and by different methods (pitfall vs. hand searching) was compared by paired *t*-tests. As very few individuals were caught by either method in the plant-year 2002 stand, data from this stand have not been included in correspondence analysis, but are included in tables of total catches. Independent-samples *t*-tests were applied to test the size tendency in correspondence analysis graphs.

Results

In total, 236 individuals of twenty-three species were caught by hand searching and pitfall trapping. Twelve species were found by both methods and eleven species were only found by one or other method. Pitfall trapping collected 188 individuals and 19 species, while hand searching produced fewer individuals (48) but only three species less.

The numbers of individuals of each species caught by the two methods are shown arranged by body size in Tables 1 and 2. *Harpalus rufipalpis* Sturm was the most abundant species caught by either method, however, its relative frequency was

Table 1. The total numbers of individuals caught by hand searching and pitfall trapping for each species less than 8 mm in length. Species are arranged in increasing size order, according to Joy (1932).

Species	Hand searching	Pitfall trapping	Size (mm)
Syntomus foveatus Fourcroy (*)	4	5	2.5–3.5
Bradycellus harpalinus Audinet-Serville	2	0	3
Bembidion lampros Herbst	0	1	3
Notiophilus biguttatus F.	2	2	3.5–5.5
Notiophilus aquaticus L.	1	13	3.5–5.5
Amara tibialis Paykull	9	6	4.5–5
Olishopus rotundatus Paykull (*)	1	0	6–7
Amara convexior Stephens (*)	1	1	7–7.5
Amara lunicollis Schiödte	4	14	7–8
Amara aenea De Geer	1	0	6–8
Total number of species	9	7	
Total number of individuals	25	42	

(*) species with British distribution mainly restricted to Breckland, according to Collier (1995) and Luff (pers. com.).

Table 2. The total numbers of individuals caught by hand searching and pitfall trapping for each species greater than 8 mm in length. Species are arranged in increasing size order, according to Joy (1932).

Species	Hand searching	Pitfall trapping	Size (mm)
Harpalus rufipalpis Sturm (*)	15	117	8–10
Pterostichus quadrifoveolatus Letzner (Nb)	3	5	8–10.5
Harpalus rubripes Duftschmid	1	1	8–11
Harpalus latus L.	1	1	8–11
Poecilus versicolor Sturm	0	1	8–11.5
Harpalus tardus Panzer	1	5	9–11
Harpalus smaragdinus Duftschmid (Nb*)	0	4	9–11
Harpalus affinis Schrank (*)	1	4	9–12
Calathus ambiguus Paykull (Nb)	1	0	10–13
Cicindela campestris L.	0	1	10.5–14.5
Harpalus rufipes De Geer	0	1	14–16
Carabus nemoralis Müller	0	2	18–28
Carabus problematicus Herbst	0	4	20–30
Total number of species	7	12	
Total number of individuals	23	146	

(Nb) Nationally Scarce B species; (*) species with British distribution mainly restricted to Breckland, according to Collier (1995) and Luff (pers. com.).

significantly greater in pitfall than in hand searching samples (62% and 31% of the total number of individuals caught by pitfall traps and hand searching: d.f. = 1, $\chi^2 = 13.7$, $P < 0.001$). Individuals of larger species ($\geqslant 8$ mm) formed the major proportion of the total catch in pitfall samples (146 larger compared with 42 smaller), in contrast, larger species contributed just less than half of the catch in hand searching samples (23 larger, 25 smaller). This size bias between the two methods was highly significant when considering the total catch (d.f. = 1, $\chi^2 = 15.2$, $P < 0.001$), however, when *H. rufipalpis* was excluded, the size bias between pitfall sampling and hand searching was non-significant (d.f. = 1, $\chi^2 = 2.0$, $P = 0.154$).

Of those species that were smaller than 8 mm (shown in Table 1), three out of nine were only found in hand searching samples, while only one species *Bembidion lampros* Herbst was found solely in pitfall traps. More individuals of *Amara tibialis* Paykull were found in hand searching than by pitfall trapping. The abundance of *Notiophilus aquaticus* L. and *Amara lunicollis* Schiödte collected by pitfall trapping was much higher than that by hand searching, with these species represented in five and eight out of the total of 45 pitfall traps, respectively.

Of the species larger than 8 mm (shown in Table 2), six out of thirteen species were only caught by pitfall trapping and only one species, *Calathus ambiguus* Paykull, was found by hand searching but not in pitfall traps. For all other larger species except for *C. ambiguus*, numbers obtained by pitfall traps were at least equal to or greater than those obtained by hand searching.

Figure 1 showed the sample of ordination in the correspondence analysis. The general pattern of habitat association in relation to the primary ordination axis was similar for the two different methods, with samples from the mature forest habitat having a markedly different species composition and occurring to the right on axis 1, and clear-fell and ride margin samples occurring towards the left. However, samples obtained by the two different methods were separated on axis 2, with hand-search

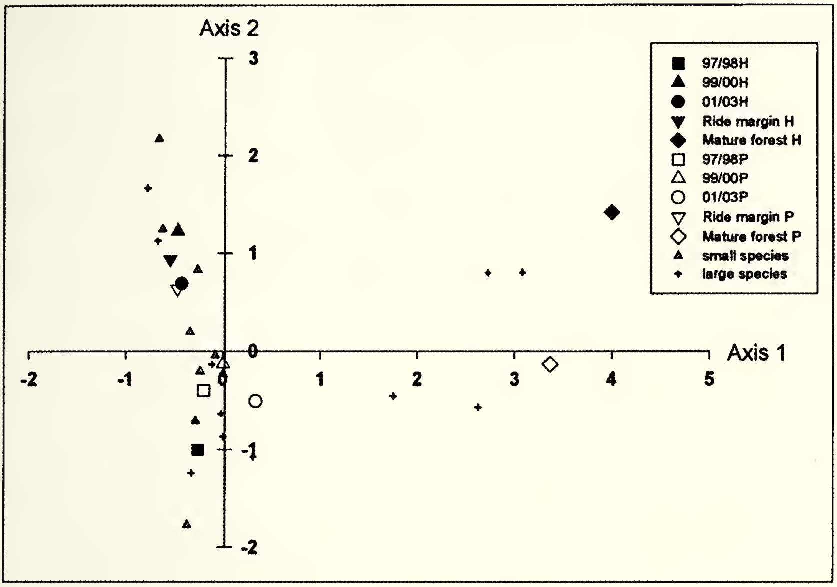

Fig. 1. Correspondence analysis of carabid composition in samples collected by hand searching and pitfall trapping with species. The first axis explained 25% of the total species variance, with axis 2 explaining an additional 16%. Numbers refer to plant years of pooled clear-fell samples. For example, 97/98 refers to a pooled sample of individuals taken from stands with planting years 1997 and 1998. H: samples taken by hand searching; P: samples taken by pitfall trapping. Beetle species were categorised as either small (<8 mm) or large ($\geqslant 8$ mm).

samples tending to be located above respective pitfall samples obtained from the same habitat (with the exception of pooled samples from 1997/98 planting years which showed the opposite trend). Carabid composition of composite samples collected from the same habitats did not differ between the two methods on axis 1 (mean $\pm$ SD for hand searching $= 0.46 \pm 1.98$; for pitfall trapping $= 0.61 \pm 1.57$; paired t-test: d.f. $= 4$, $t = -0.623$, $P = 0.567$), or on axis 2 (mean $\pm$ SD for hand searching $= 0.65 \pm 0.97$; for pitfall trapping $= -0.11 \pm 0.45$; paired t-test: d.f. $= 4$, $t = 1.89$, $P = 0.132$).

Most of the small-sized species were located at the mid to upper part of axis 2, with the exception of *Amara aenea* De Geer. In contrast, larger species tended towards the lower part of the ordination, with the exception of *C. ambiguus* and *Cicindela campestris* L. However, overall, larger and smaller species did not differ significantly in their location on axis 2 (mean $\pm$ SD for smaller species $= 0.37 \pm 1.25$; for larger species $= -0.15 \pm 0.93$; d.f. $= 21$: $t = 1.44$, $P = 0.265$). The four species near mature forest samples were *Carabus problematicus* Herbst, *Carabus nemolaris* Müller, *Harpalus latus* L. and *Pterostichus quadrifoveolatus* Letzner. They were all found in mature forest samples, by either one or both methods.

Figure 2 showed the results of correspondence analysis with *H. rufipalpis* excluded. By comparing Figures 1 and 2, the distance between the mature forest samples and those from clear-fell habitats was reduced. Most of the smaller species were located from the mid to the right hand side of the ordination compared with the larger

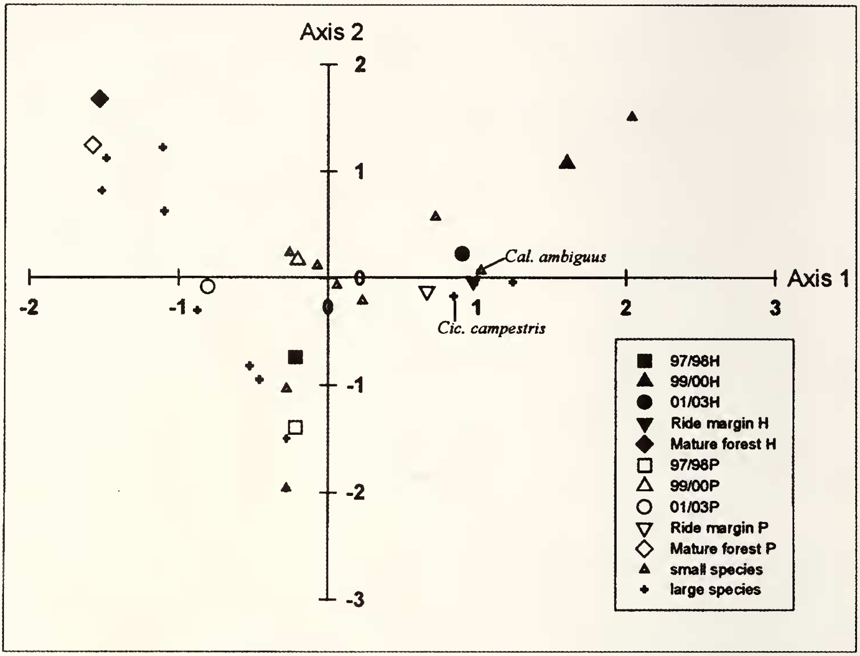

Fig. 2. Correspondence analysis of carabid composition in samples collected by hand searching and pitfall trapping, performed on species matrix excluding *Harpalus rufipalpis*. Beetle species were categorised as either small (<8 mm) or large (≥8 mm). The first axis explained 21.4% of the total species variance, with axis 2 explaining an additional 17.6%. Explanations of legends see Fig. 1.

species which were located to the left, with the exception of *C. ambiguus* and *C. campestris*. The difference in location of species from the two carabid size groups was significant (axis 1 scores, mean ± SD for smaller species = 0.52 ± 0.91; for larger species = −0.48 ± 0.85; d.f. = 20; $t = 2.69$, $P = 0.014$). Similarly, hand searching samples were located to the right of their respective pitfall samples. This trend was not so obvious in 1997/98 samples, but they were not as exceptional as the pattern shown in Figure 1. The carabid composition obtained by the two different methods showed no significant differences on axis 1 (mean ± SD for hand searching = 0.35 ± 1.24; for pitfall trapping = −0.43 ± 0.83; paired *t*-test: d.f. = 4, $t = 1.91$, $P = 0.128$), but this difference was significant on axis 2 (mean ± SD for hand searching = 0.44 ± 0.95; pitfall trapping = −0.04 ± 0.94; paired *t*-test: d.f. = 4, $t = 3.43$, $P = 0.027$).

Discussion

In total, twenty-three species were caught in this study, representing 31% of the known Thetford Forest carabid fauna (Y. C. Lin, unpublished data). Among the 23 species, three are categorised as Nationally Scarce B: *P. quadrifoveolatus*, *Harpalus smaragdinus* Duftschmid and *C. ambiguus* (Hyman & Parsons, 1992) and six, including *H. smaragdinus*, have their UK distribution restricted to the Breckland

(Tables 1 and 2). These eight species are all associated with heathland or sandy habitats, though some also occur in other habitats, such as *P. quadrifoveolatus* which occurs in woodland, and *H. smaragdinus* which favours arable fields (Luff, 1998). Other sandy, heathland or moorland affiliates found in this study include *C. campestris* (Field Tiger Beetle), *A. tibialis* and *N. aquaticus*. The Breckland region has long been known to support scarce species of disturbed and sandy habitats, including species normally associated with coastal dunes (Morley, 1908; Telfer & Eversham, 1996). However, the once extensive heathland of Breckland has been greatly reduced by coniferous afforestation and conversion to arable fields (Dolman & Sutherland, 1992) and the persistence of scarce sandy and heathland species in the converted areas needs further investigation.

The effort of taking hand searching samples is greater than that of pitfall trapping, however, a greater volume of material was obtained by pitfall sampling. The hand searching samples took a total of 40 people-hours, while pitfall samples were collected by one person in six hours. Despite the markedly lower sampling effort, the pitfall traps provided more than three times the number of individuals obtained by hand searching. This advantage of pitfall trapping explains why it is one of the most frequently used sampling methods in research on carabids (Thiele, 1977; Desender & Maelfait, 1986).

There was a tendency for pitfall samples to be dominated by larger species. This size bias was non-significant when the total catch was considered after exclusion of *H. rufipalpis* (χ^2-test). However, when the species composition in different habitats was considered, the location of samples obtained by the two methods differed significantly (*t*-test on axis 2 scores in Fig. 2). A similar phenomenon has also been observed by other researchers. Arneberg & Andersen (2003) found the slopes of size-abundance relationships using data from pitfall traps were significantly more positive than those from hand searching. By comparing samples taken from litter washings, Spence & Niemelä (1994) also found pitfall trap catches to be biased toward larger carabids. A number of possible explanations for the apparent bias can be considered. Firstly, although hand searching was intended as a true measure of absolute density, large nocturnal burrow-forming carabids may be under-represented in diurnal samples compared with their true abundance in a particular habitat. Secondly, larger carabid species may be more active than smaller ones and therefore more likely to be caught in pitfall traps (Spence & Niemelä, 1994). For example, large carnivorous carabids such as *Carabus* spp. tend to move more because their food resource is more scattered (Andersen, 1995). Finally, the smaller carabid species may be capable of entering, but then climbing out of pitfall traps (Hawthorne, 1994). Although smaller carabid species tended to be relatively less abundant in pitfall samples compared with hand searching samples, two smaller species, *A. lunicollis* and *N. aquaticus* were much more common in pitfall than handsearch samples. It is possible that these two species were preferentially captured due to a behavioural response to the glycol preservative.

The high representation of *H. rufipalpis* in pitfall compared to hand searching samples, was a major factor contributing to the size bias in pitfall trapping. Over-representation of certain species has also been found in previous research. Desender & Maelfait (1986) suggested the overestimation of some observed species (*Bembidion properans* Stephens, *B. lampros*, *Loricera pilicornis* F. and *A. aenea*) was due to their high mobility and active hunting during daytime. Andersen (1995) found that *Bembidion schuppelii* Dejean was over-represented in sub-optimal microhabitats, which was in accordance with the results of Grüm (1971) who found that the activity of satiated individuals was higher in sub-optimal than in optimal habitats (Andersen, 1995).

The species composition of pitfall samples was dominated by *H. rufipalpis*, and the ordination gave a qualitatively different result when this species was excluded. With *H. rufipalpis* included, the primary correspondence analysis axis represents a marked contrast between mature forest and all other habitats, while the contrast between sampling methods was reflected on the secondary correspondence analysis axis (Fig. 1). Excluding *H. rufipalpis*, although the location of the mature forest samples still contrasted with that of the other habitats, this dichotomy was less extreme. This might be due mainly to the absence of *H. rufipalpis* in mature forest samples and with this species excluded, the differences between samples obtained by the two methods were apparent on the primary correspondence analysis axis (Fig. 2). Despite this, the community structure revealed by the ordinations was broadly similar for both methods. This shows that the differences in carabid compositions taken from extremely different habitat structures (mature forest vs. open clear-felled and re-stocked habitats and ride margins) was revealed by both sampling methods. However, the two methods differed in the manner in which they represented carabid species composition between samples taken from structurally similar habitats. The correspondence analysis composition of carabid samples collected by these two methods did not differ significantly when *H. rufipalpis* was included, but the difference on axis 2 was close to significant. After the exclusion of this species, axis 2 scores of samples obtained by the two methods differed significantly.

To conclude, the popularity of pitfall trapping is easily understood by its much greater catching rate compared with hand searching. For the relative composition of the carabid assemblage in different habitats, the major pattern of results gained from pitfall trapping reflected those from hand searching, but some differential biases of the two methods remain apparent. The tendency to catch larger species in pitfall traps and the over-representation of some species such as *N. aquaticus*, *A. lunicollis* and *H. rufipalpis*, re-emphasise the need for caution in the interpretation of community composition from pitfall results.

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